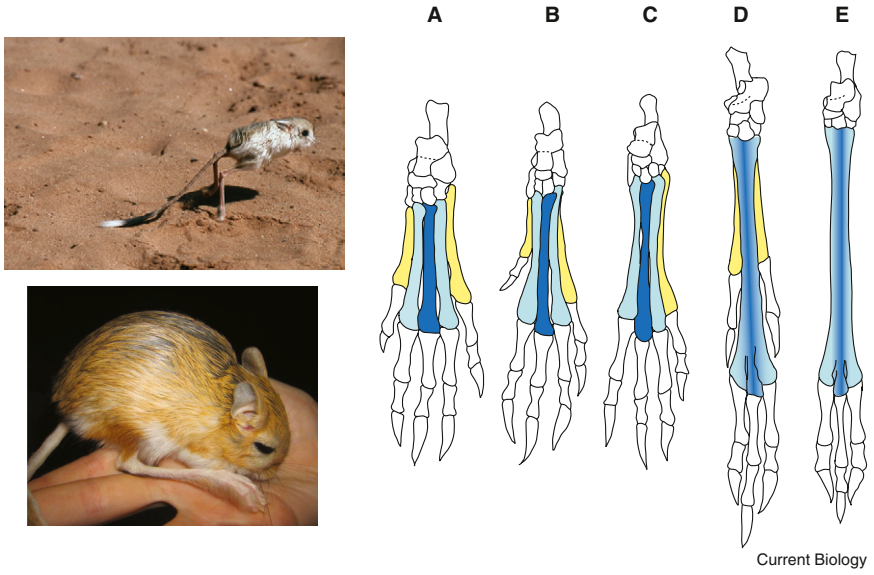

Figure 5. Digit reduction in desert-dwelling rodents.

(A) Gerbil (*Meriones sp.*). (B) Ord's kangroo rat (*Dipodomys ordii*). (C) Merriam's kangaroo rat (*Dipodomys merriami*). (D) Jerboa (*Allactaga sp.*). (E) Greater Egyptian jerboa (*Jaculus orientalis*). Digits I and V are shown in yellow; digits II, III, and IV are shown in blue. *Allactaga* and *Jaculus orientalis* have lost digits I and V, and digits II, III, and IV have fused together. (Adapted with permission from Berman 1985 / Blackwell publishing.) Photograph of a Desert kangaroo rat provided by E. Bartov (top); photograph of a Northern three-toed jerboa provided by K. Cooper (bottom).

storage and circadian rhythms. Memory and learning have been studied in squirrels that cache their food, sometimes not returning until the next year. Singing mice provide a new model for studying speech and learning. Studies of wild rodents will undoubtedly give us a window into the genetics underlying phenotypic variation, further promoted by genome sequencing projects that extend beyond the usual model species (see *www.genome.gov*).

All of this diversity can be traced back to the first fossil rodents (Ischyromyoidae) from the late Paleocene of Asia. These primitive rodents, although donning a beaver-like skull, had the teeth and feet of a squirrel, and skeletal features suggestive of an arboreal lifestyle. And from so squirrely a beginning evolved endless rodential forms most beautiful — species as distinct as ungulate-like capybaras, raccoon-like viscachas, rabbit-like springhares, and otter-like muskrats. Rodents are an evolutionary success story—they were here long before us and these opportunistic survivors will certainly be here long after we are gone.

Further reading

Animal Diversity Web: http://animaldiversity.ummz.umich.edu/site/accounts/information/Rodentia.html.

Beck, R.M.D., Bininda-Emonds, O.R.P., Cardillo, M., Liu, F-G.R., and Purvis, A. (2006). A higher-level MRP supertree of placental mammals. BMC Evol. Biol. *6*, 1–14.

Berman, S.L. (1985). Convergent evolution in the hindlimb of bipedal rodents. Zeit. Zoolog. Systemat. Evolutions *23*, 59–77.

Carleton, M.D. (1984). Introduction to rodents. In Orders and Families of Recent Mammals of the World, S. Anderson and J.K. Jones, Jr. (eds). (New York: John Wiley & Sons) pp. 255–265.

MacDonald, D. (2001). Encyclopedia of Mammals. (Oxford: Oxford University Press.)

Nowack, W.M. (1991). Walker's Mammals of the World. (Baltimore: John Hopkins University Press.)

Steppan, S.J., Adkins, R.M., and Anderson, J. (2004). Phylogeny and divergence-date estimates of rapid radiations in muroid rodents based on multiple nuclear genes. Syst. Biol. *53*, 533–553.

Vaughan, T.A., Ryan, J.M., and Czaplewski, N.J. (2000). Mammalogy. 4th Edition. (Philadelphia: Saunders College Publishing.)

Wilson, D.E., and Reeder, D.M. (2005). Mammal Species of the World: A Taxonomic and Geographic Reference. 3rd edition. (Washington: Smithsonian Institution Press.)

Wolff, J.O., and Sherman, P.W. (eds). (2007). Rodent Societies: an ecological and evolutionary perspective. (Chicago: University of Chicago Press.)

Department of Organismic and Evolutionary Biology and The Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, USA.
E-mail: [1]ekay@oeb.harvard.edu; [2]hoekstra@oeb.harvard.edu

Correspondences

Perceptual processing is facilitated by ascribing meaning to novel stimuli

Gary Lupyan and Michael J. Spivey

Can the *interpretation* of a visual stimulus (normally conceived as a late visual process) influence the *recognition* of that same stimulus (normally conceived as an early visual process)? Access of meaning from vision can be extremely rapid [1–3]. If the visual processing of meaningful stimuli is supported by top-down feedback from conceptual representations [4,5], then meaningful stimuli may be processed more efficiently than meaningless stimuli. A difficulty with testing this prediction is that meaningfulness is often confounded with familiarity. It is well established that familiar stimuli are easier to process than unfamiliar stimuli [6]. In visual search tasks, finding a target among unfamiliar non-targets (such as Ƨs) is much more effortful than searching among familiar non-targets (such as Ns) [7]. However, poor performance on unfamiliar stimuli may be due, not only to inexperience with them, but also to a failure to represent them as members of meaningful categories. If so, then ascribing meaning to otherwise unfamiliar stimuli should facilitate perceptual processing. We report here data from experiments using a visual search task which show that, when perceptually novel stimuli are treated as members of a known category, they are processed more efficiently. These results are simulated by a model implementing top-down feedback from category representations to visual features.

Participants (N = 62, ages 18–22) searched for the perceptually novel symbols ⊔⊓ and ⊓⊔. These symbols are 90° rotations of the numerals 5 and 2 rendered in a 'digital' font. This simple rotation reduces search efficiency by a factor of two [8], while preserving the low-level visual properties of the familiar upright numerals. To investigate whether differences in processing efficiency hinge on differences in

meaningfulness, participants were randomly assigned to one of two groups. Participants in the *number* group were instructed to think of the items as rotated 2s and 5s; participants in the *symbol* group were not. This paradigm allowed us to manipulate meaningfulness while keeping perceptual novelty constant.

Participants completed two search phases in counterbalanced order (240 total trials) searching for a ⊓⊔ among ⊔⊓'s and vice versa (Figure 1A). On each trial, participants were asked to give a target-present or target-absent response while maintaining central fixation. After the experiment, participants were given a questionnaire asking whether they thought of (or mentally labeled) the stimuli as any kind of alphanumeric characters. The responses yielded three subgroups in the *symbol* group: those who spontaneously used their own labels for the stimuli consistently (*N* = 14), or inconsistently (*N* = 11), or not at all (*N* = 16). The *number* group yielded two subgroups: those who reported consistently thinking of the stimuli as rotated 2s and 5s, as instructed (*N* = 16), and those who did not label the stimuli despite the instructions (*N* = 5).

Analysis of the randomly assigned *symbol* and *number* groups revealed that participants in the *symbol* group had significantly slower reaction times than those assigned to the *number* group, target-present trials (Figure 1B). Moreover, participants' reports of whether they conceived of the shapes as familiar characters predicted performance. Participants who were assigned to the *number* condition, or who spontaneously and consistently ascribed meaning to the stimuli, had significantly faster reaction times (*M* = 1.115 ms versus *M* = 1.431 ms), and searched more efficiently (47 ms per item versus 66 ms per item) than participants who treated the stimuli as meaningless. (For additional analyses, including error data, see the Supplemental data available on-line.)

To outline a possible mechanism for the neural components involved in this perceptual facilitation induced by stimulus meaningfulness, a localist attractor network that has successfully simulated reaction times during search [9] was modified to include an additional 'category label' component (Figure 1C). When activated, the category label provides top-down feedback to features associated with

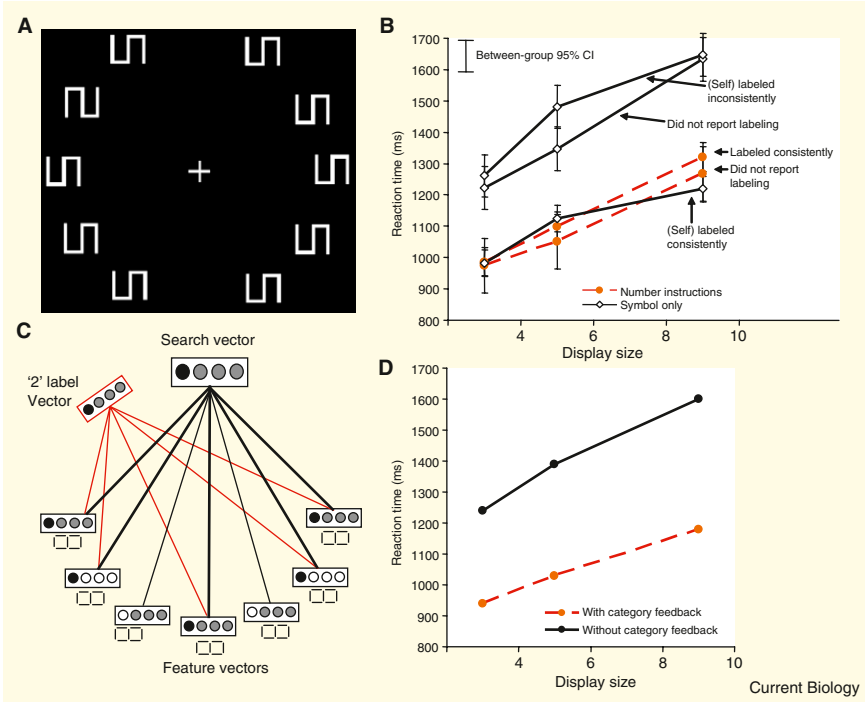

Figure 1. Results of the search trials.

(A) A sample search trial. (B) Mean reaction times (±95% CI) as a function of assigned condition (number versus symbol) and group based on questionnaire responses. Faster and more efficient performance is observed for participants who are told to think of the stimuli as rotated numerals (number condition), and for participants who, without the experimenter's instructions, consistently thought of the stimuli as meaningful. (C) Schematic of the localist attractor network simulating category influences (red component) on search for a ⊓⊔ among three ⊔⊓'s. Darker nodes are more active. Thick lines indicate strong attentional weights (connected to the orthographic features of a ⊓⊔). (D) Simulated reaction times from the network when the category component is activated (stimuli treated as meaningful) and when it is deactivated.

the target category. Each display was represented by seven feature vectors (each having as many nodes as stimuli in the display) that normalize their activation patterns to sum to 1.0, and then compute a weighted average at the search vector. During search for a ⊓⊔ among ⊔⊓'s, the five thick connections in Figure 1C (features that are associated with the target) indicate stronger attentional weights, and the two thin connections (features uniquely associated with the non-targets) indicate weaker attentional weights. The search vector then sends feedback to the feature vectors by multiplying itself by the input that just traveled up from that feature vector. The feature vectors accumulate that feedback, and then re-normalize to begin a new time cycle.

Without the top-down feedback from the category layer, the network produces a search slope of 60 ms per item. When the label layer is allowed to modulate the activity of the feature vectors with which it is associated (red lines in Figure 1C), the search efficiency is improved to 41 ms/item (Figure 1D). Thus, as the label vector gradually becomes more confident that the target is present, its feedback subtly biases the feature vectors toward the target node (see Supplemental data for code).

Considering novel stimuli as instances of familiar categories significantly improved mean search times, search efficiency, and reduced false alarms (Figure S3 in the Supplemental data). Thus, ascribing meaning to perceptually unfamiliar stimuli improved visual processing. This facilitation can be modeled by a simple attractor network in which top-down feedback from category labels recurrently sharpens the distributions of activation within the feature vectors. The present findings are compatible with a range of theoretical accounts of reentrant visual processes [5,10,11]. Although the neural locus of the reported effect remains unspecified, a candidate lies in the cortico-cortical projections between the orbitofrontal (OFC) and inferotemporal (IT) cortex, with OFC providing prediction signals to IT [12]; this feedback is predicted to be more robust for meaningful objects.

Our findings demonstrate a possible behavioral outcome of a visual system with massive retrograde connections between category-sensitive and more primary visual areas [5,12] and suggest a reassessment of theories that eschew top-down conceptual influences on visual selection [13,14]. The present results make it clear that visual perception depends not only on what something looks like, but also on what it means.

Supplemental data

Supplemental data are available at http://www.current-biology.com/cgi/content/full/18/10/R410/DC1

Acknowledgements

This work was supported in part by an NSFGRF to G.L. and NSF-BCS-0721297 to M.S.

References

1. Dell'Acqua, R., Pesciarelli, F., Jolicoeur, P., Eimer, M., and Peressotti, F. (2007). The interdependence of spatial attention and lexical access as revealed by early asymmetries in occipito-parietal ERP activity. Psychophysiol *44*, 436–443.
2. Grill-Spector, K., and Kanwisher, N. (2005). Visual recognition - as soon as you know it is there, you know what it is. Psychol. Sci. *16*, 152–160.
3. Fabre-Thorpe, M., Delorme, A., Marlot, C., and Thorpe, S. (2001). A limit to the speed of processing in ultra-rapid visual categorization of novel natural scenes. J. Cogn. Neurosci. *13*, 171–180.
4. McClelland, J.L., and Rumelhart, D.E. (1981). An interactive activation model of context effects in letter perception. 1. An account of basic findings. Psychol. Rev. *88*, 375–407.
5. Mumford, D. (1992). On the computational architecture of the neocortex II. The role of cortico-cortical loops. Biol. Cybernet. *66*, 251.
6. Frith, U. (1974). Curious effect with reversed letters explained by a theory of schema. Percept. Psychophys. *16*, 113–116.
7. Wolfe, J.M. (2001). Asymmetries in visual search: An introduction. Percept. Psychophys. *63*, 381–389.
8. Wang, Q.Q., Cavanagh, P., and Green, M. (1994). Familiarity and pop-out in visual search. Percept. Psychophys. *56*, 495–500.
9. Reali, F., Spivey, M., Tyler, M., and Terranova, J. (2006). Inefficient conjunction search made efficient by concurrent spoken delivery of target identity. Percept. Psychophys. *68*, 959–974.
10. Di Lollo, V., Enns, J.T., and Rensink, R.A. (2000). Competition for consciousness among visual events: The psychophysics of reentrant visual processes. J. Exp. Psychol. Gen. *129*, 481–507.
11. Lamme, V.A.F., and Roelfsema, P.R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. Trends Neurosci. *23*, 571–579.
12. Kveraga, K., Ghuman, A.S., and Bar, M. (2007). Top-down predictions in the cognitive brain. Brain Cogn. *65*, 145–168.
13. Theeuwes, J. (1993). Visual selective attention - a theoretical analysis. Acta Psychol. *83*, 93–154.
14. Pylyshyn, Z. (1999). Is vision continuous with cognition? The case for cognitive impenetrability of visual perception. Behav. Brain Sci. *22*, 341–365.

Department of Psychology, Cornell University, Ithaca, New York 14853, USA.
E-mail: il24@cornell.edu

Saccadic latency during electrical stimulation of the human subthalamic nucleus

Yasin Temel[1,2,4], Veerle Visser-Vandewalle[1,4] and R.H.S. Carpenter[3]

High-frequency electrical stimulation of the subthalamic nucleus ('deep brain stimulation') has rapidly become a popular method for treating patients with Parkinson's disease [1], and is now widely recognised as one of the most effective long-term treatments. So far, the neural mechanisms underlying its effectiveness have been elusive. However, measuring saccadic latency — the time taken to look at a sudden visual stimulus — seems a promising approach. Latency varies randomly from trial to trial, and analysis of the resultant statistical distributions

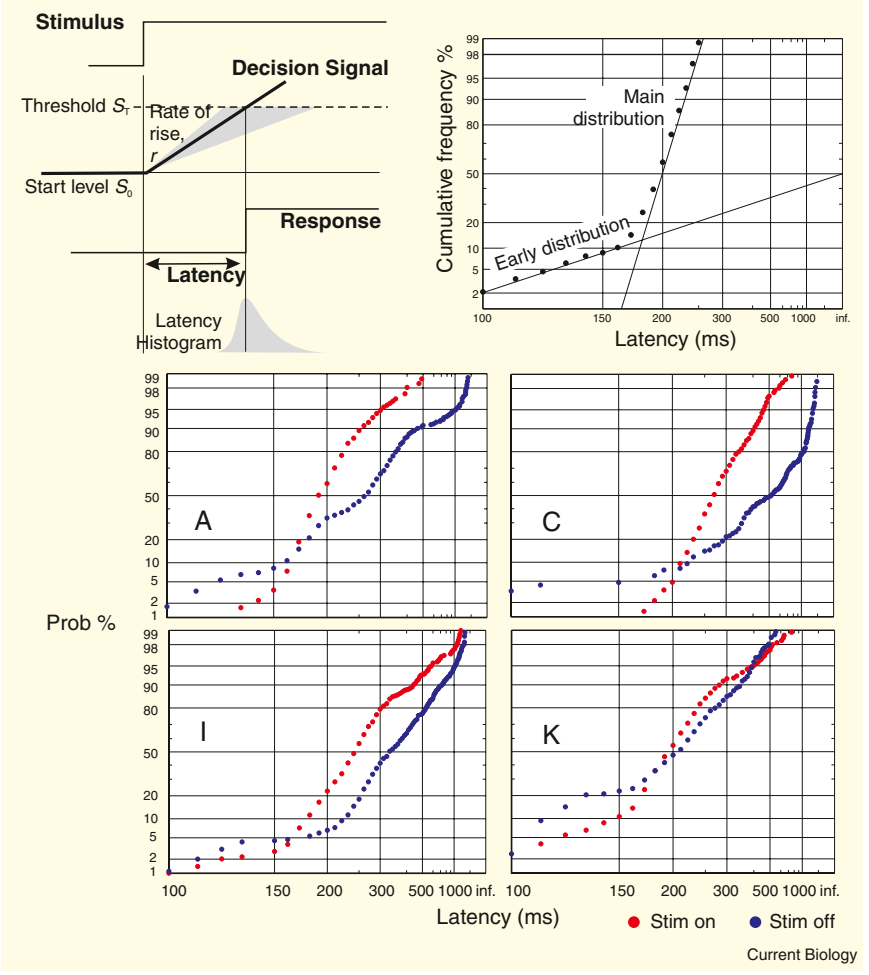

Figure 1. Saccadic latency distributions.

Above: in the LATER model, a decision signal rises linearly from its initial value of S_0 at a rate r until it reaches a threshold level S_T, at which point a response is initiated. Because r varies randomly (following a normal distribution) on different trials, the time to reach threshold, and thus the latency, also varies randomly. Consequently, if reciprocal saccadic latencies are plotted as a cumulative histogram, using a probit ordinate, a straight line will be obtained (right). However, under certain conditions more saccades with very short latencies are observed than the model would predict: these generally lie on a different line of shallower slope that intersects it. Below: reciprobit plots for four representative patients, comparing all trials for which the subthalamic stimulation was on, with all trials in which it was off. The effect of stimulation is to reduce median latency, the proportion of early responses, and the degree of irregularity of the distributions.